STUDIA FORESTALIA SUECICA

Nr 96 · 1972

Studies on the basic density in mother trees and progenies of pine

Studier över torr-råvolymvikt hos moderträd och avkommor av tall

ANDERS PERSSON
Department of Forest Yield Research

SKOGSHÖGSKOLAN
ROYAL COLLEGE OF FORESTRY
STOCKHOLM

Abstract

ODC 812.31 + 165.3 — — 174.7 Pinus silvestris (485)

The basic density is a highly important wood property, not least for pulping purposes. The possibilities of selection improvement in respect of basic density in pine (Pinus silvestris L.) are studied in this paper.

The method of calculating the stem density in young pines by means of the basic density of branches is shown to have low precision.

*In a comparison of the density in progenies with that in mother trees in two groups of material, correlation coefficients of 0.591*** (29 pairs of values) and 0.415 (22 pairs of values, not significant) were obtained. A calculation of the heritability (H) on the basis of the regression of progenies on mother trees gave for the material in question the values $H = 0.56$ and $H = 0.46$ respectively.*

Ms. received 27 oktober 1971

Allmänna Förlaget
ISBN 91-38-00223-X
Esselte Tryck 1972

Contents

1 Introduction 5
2 Intention 6
3 Previous investigations 7
4 Relationship between basic density in stem and in branches 9
4.1 Preliminary investigation 9
4.2 Collection of material from progeny trials 9
4.3 Relative basic density 9
4.4 Statistical analyses 10
4.5 Applications 11
4.6 A comparison between progenies . . 12
5 Comparison between progenies and mother trees 13
5.1 Collection of material 13
5.1.1 Background 13
2 Description of progeny trials 13
3 Sampling in the progeny trials . . . 13
4 Sampling from the mother trees . . . 14
5.2 Laboratory treatment 14
5.3 Treatment of data 14
5.4 Relative basic density 14
5.4.1 General 14
2 Progeny trials 14
3 The mother trees 14
5.5 Progeny differences 17
5.6 Relationship between basic density in progenies and mother trees 18
5.6.1 Tests of significance 18
2 Selection effects 19
6 Discussion 21

Summary 24
Acknowledgement 26
Literature 27
Sammanfattning 29
Figures 30
Tables 34
Appendices 36

1 Introduction

A problem which comes to the fore in the assessment of the wood quality of a tree is that of finding clearly definable and easily measurable characteristics by means of which a reliable and objective measure of the tree's usefulness for various purposes may be obtained. This question has come to be of especial importance in recent years, since an increasing amount of work has gone into forest tree breeding. In this context it is of particular importance to obtain appropriate measures of the parent trees' quality. As progeny trials reach an age at which they may be assessed, for these too is it of prime importance to have reliable, objective measures of quality.

Throughout the world today the pulp and paper industry is expanding and becoming ever more dominant amongst the forest processing industries. Because of this development it is increasingly important to find good measures of the quality of a tree from the pulping point of view. The attributes most used have been the density (dry wt/dry volume) and basic density (dry wt/green volume) of the wood.

Earlier investigations usually made use of the density, whereas more recently basic density has largely been employed. The reason for this is that pulpwood is customarily measured at a moisture content above the fibre saturation point, hence basic density gives a better picture of the dry matter content per unit volume. Furthermore, the green volyme may be more reliably measured than the dry. This is especially true of large samples, which readily form internal fissures on drying, their volume being overestimated in consequence.

On the whole, these two densities are in fair agreement, a high density being associated with a high basic density in one and the same tree species.

Many investigations have been made of the influence of density both on the attributes of the sawn timber and on the pulp yield's quantity and quality. Some of these results are compiled in Ericson (1961), and show that with increasing basic density and density there is associated an increase in all the strength properties of the knot-free sawn timber. The pulp yield as expressed in kilograms of dry pulp per unit volume wood increases with increasing density. The tearing strength in the manufactured paper increases with increasing density, while the tensile strength and bursting strength decrease (Nylinder & Hägglund 1954). On the assumption that wood is valued by volume, the pulp yield is most important.

2 Intention

The aim of this study is to discover whether any connection exists in pine between the basic density of the wood of the mother trees and that of the progeny after free pollination.

In this context it is important that the density of the progeny be determined at as early an age as possible. Whether a clear relationship exists or not, it is of great value to be able to compare at an early stage the progeny with respect to basic density. It would hence be possible rapidly to rank the mother trees by reference to the basic density of the progeny.

At present, density may determined with the aid of increment cores. This requires the progeny to have attained sufficient dimensions to permit boring; this implies a loss of time. Furthermore, the young trees are undoubtedly disturbed by boring, which can affect other comparisons between the progenies. For these reasons the possibility of determining the density of the stem through the density of the branches was first studied.

The main part of the investigation comprises direct comparisons between the density of the mother trees and that of the progenies. Strong correlation between these densities implies that trees with a heritable tendency to form wood of low density may be eliminated at the time when the mother trees are selected. At present the Coordination Committee for Forest Genetics and Tree Breeding carries out a routine determination of the basic density of the proposed mother tree. In the final assessment of the trees the density is then included as one of many factors which are evaluated to give a final rating.

If co-variation exists between the density of the mother trees and that of the progenies this means that there is reason to pay attention to the density of the mother trees.

3 Previous investigations

The relationship between the density in the stem and in branches of the loblolly pine (*Pinus taeda* L.) has been studied in investigations in the United States. Zobel & Rhodes (1956, 1957) found strong relationships between the basic density in the innermost eight annual rings and the density in the older wood of the same tree (correlation coefficient 0.80—0.85). They also found a fairly good correlation (correlation coefficient 0.55—0.70) between the density in branches taken from breast height on trees three to nine feet tall, and the density in the stem as calculated for the wood at the base of the branches in question. The authors considered branch investigation to be a feasible method for estimating the basic density in the stems of young trees.

Jackson & Warren (1962) found highly significant correlation coefficients for the relationship between the density in two-year-old branch wood and the density in stem wood (r=0.68 and 0.80). In slash pine, too, (*Pinus elliottii* Engelm.) this relationship was highly significant (r=0.73). Jackson & Warren also studied the density relationship between mother trees and progenies and obtained a correlation coefficient of 0.87. However, for this purpose the two species were united into one group, which makes for difficulties in assessing the value obtained.

In slash pine the relationship between the density of the mother trees and the density in the progenies after free pollination has also been investigated by Goddard & Cole (1966). These authors found, amongst other things, that it was immaterial whether the investigation was made on wood free from or wood containing extractives. After the adjustment of the mother trees' densities in respect of the mean value for each growing site, and subsequent comparison with the mean value for density in the various progenies a significant regression was obtained which explained 24 per cent of the variation amongst the progenies; this implies a correlation coefficient of ca 0.50. Goddard & Cole suggested a combined selection, meaning that of 12 progenies in an experiment they chose four in which both the mother tree and the progeny had a density greater than the average. By this means the average density of the progenies could be increased by 2.5 per cent.

In numerous investigations in comparative progeny trials the heritability (degree of heritability in narrow sense, H or h^2) for the density has been determined for e.g. *Pinus taeda, P. radiata* and *P. elliottii* (van Buijtenen 1962, Squillace et al. 1962, Goggans 1964, Goddard & Cole 1966, Stonecypher 1966, Stonecypher & Zobel 1966). The basis for these have been comparative field experiments, where, by means of an analysis of variance, the components of variance within and between progenies have been allocated. The values obtained for heritability lie within the interval 0.2—1.0. Hattemer (1963) considers that heritability calculated in this fashion is more a parameter for field trials than a genetical parameter. Heritability may also be calculated, according to Hattemer, from the regression of progeny on parents, so that after free pollination that relationship may be employed whereby the obtained regression between progenies and mother trees gives half the value of the heritability. He does not, however, consider even this method ideal, partly because one is forced to compare individuals of very different ages, growing, as a rule, in very dissimilar environments.

Harris (1965) holds that the heritability as calculated by analysis of variance is valid only under the specific conditions obtaining in the field trial in question and thus can not be considered a definite characteristic

of a certain species. The same views are discussed by Zobel (1960, 1961, 1963) and are dealt with in greater detail in chapter 6 of the present work.

Harris also points out that the density is not a simple attribute in the biological sense but is, rather, dependent on many factors, each one controlled by a more or less complex physiological system. Experience from other biological material has, however, shown that selection in respect of similarly complicated end products (e.g. yield of seed) can give satisfactory results.

4 Relationship between basic density in stem and in branches

4.1 Preliminary investigation

For the investigation were chosen 20 ca 12-year-old pines. From each tree samples were taken both from the stem and from the branches. In all, eight stem samples and 35 branch samples were collected per tree. For each sample the basic density was determined by the method described in Appdx 1. The relative density was not calculated, for reasons which will appear from Appdx 2. The correlation coefficients were calculated for the relationship between the basic density of the various branch parts and the density of a six-year-old stem section. Those branch samples which exhibited the highest correlation coefficient were partly two-year-old branch sections in the second branch whorl from above ($r=0.46$—0.56, depending on the ranking in length) and branches in the topmost whorl ($r=0.28$—0.47). It was decided that in further investigations samples should be taken from these branches. Stem samples should be taken from a six-year-old stem section.

4.2 Collection of material from progeny trials

The collection of material for the second stage of the work was undertaken in a progeny trial in northern Värmland (latitude 60°30′N, height above sea level ca 400 m). The experiment was established by the Association for Forest Tree Breeding and has the designation No. 48 Filphus.

The experiment was established with the intention of comparing the progenies from free pollination of 22 plus trees. There were, furthermore, progenies from three populations. The trial is intended to comprise both the quantitative and the qualitative development. No determination of the densities had preceded the choice of plus trees.

The experimental area is divided into four blocks of 60×60 m, which in their turn are divided into 25 plots, one for every progeny. The progenies are distributed randomly in each block. The plots are planted with 100 trees at the spacing 1.2 m. Buffer strips exist only round the outer margin of the experimental area, and not between blocks and plots.

The area was planted in 1952 with 2 +1 pine. The trees had thus passed through 14 growing seasons. Their height varied from 1—4.5 m. No clear differences in growth, colour, etc., between progenies were observable.

Samples were taken from five trees per plot, i.e. from 20 trees per progeny or 500 trees in all. Within the plots where primarily selected trees which had already been chosen on the map of the experiment. If any of these was unsuitable for sampling, then from amongst the surrounding trees another was selected according to a pre-determined system. The trees thus chosen could be considered as a systematic sample of the population. From each tree samples were taken according to 4.1.

4.3 Relative basic density

The reason for the calculation of the relative basic density will be apparent from Appdx 2.

The regression functions for calculation of the relative basic density were based on the relationship between the samples' basic density and diameter. Since the age was constant for every sample type, diameter could be used as a measure of the annual ring width.

The following equations were obtained:

y = basic density, g/cm³,
x = diameter, tenths of mm,
r = correlation coefficient

Type of sample	Equation	r	
Stem	$y = 0.394\,149 - 0.000\,170\,x$	—0.510	(1)
1-year-old branch section	$y = 0.290\,581 - 0.000\,328\,x$	—0.170	(2)
2-year-old branch section	$y = 0.380\,352 - 0.000\,610\,x$	—0.383	(3)

With the aid of these functions a calculated value for the basic density was obtained for each individual sample. The relative basic density was calculated as 100 × observed basic density/calculated basic density for every sample. The mean and standard deviation of the basic density for every individual progeny may be found in Persson (1968, Table 4).

4.4 Statistical analyses

The correlation between the basic density in the stem and in the one-year-old branch and in the stem and in the two-year-old branch, has been calculated for every progeny. The coefficients for both the observed and the relative densities are compiled in Persson (1968, Table 5).

The regression coefficient for density in the stem on density in the branches has also been calculated for all progenies. The values obtained are given in the above-mentioned table.

For the whole material the following equations and correlation coefficients (r), y = density in the stem, x = density in branch were obtained.

All correlation coefficients are highly significantly greater than 0.

The material was subsequently processed with the aid of the covariance analysis given in Bonnier & Tedin (1940, pp. 142—155). The following analyses were attempted:

I. Investigation of the position of the progenies relative to their mean regression line.
II. Testing of the regression coefficients of the individual progeny.

Significance obtained in any of these tests indicates that the various progenies cannot be ascribed to the same population as regards the co-variation between basic density in the stem and in branches. The tests were performed for the following four regressions: Stem on one-year-old branch sections and stem on two-year-old branch sections for observed and relative basic density.

The covariance analysis was performed with a simple grouping in which the trees within a progeny represent one group. The analysis is described in Persson (1968, Table 6—7). A summary of these tables is given below.

	Regression of	Equation	r	
Observed basic density, g/cm³	stem on 1-year-old branch section	$y = 0.4836\,x + 0.2025$	0.345	(4)
	stem on 2-year-old branch section	$y = 0.5698\,x + 0.1419$	0.487	(5)
Relative basic density, %	stem on 1-year-old branch section	$y = 0.3340\,x + 66.373$	0.335	(6)
	stem on 2-year-old branch section	$y = 0.3922\,x + 60.815$	0.356	(7)

I. The scatter of the mean values for the progeny around the mean regression line "within progenies". No. of degrees of freedom in the numerator 24, in the denominator 474.

	Variance ratio
Observed basic density, regression:	
stem on 1-year-old branch section	3.390***
stem on 2-year-old branch section	4.061***
Relative basic density, regression:	
stem on 1-year-old branch section	3.500***
stem on 2-year-old branch section	3.831***

II. Comparison between the slope of the regression line for the individual progenies. No. of degrees of freedom in numerator 24, in denominator 450.

	Variance ratio
Observed basic density, regression:	
stem on 1-year-old branch section	0.935
stem on 2-year-old branch section	1.315
Relative basic density, regression:	
stem on 1-year-old branch section	0.595
stem on 2-year-old branch section	1.119

For all four relationships tested the following holds: The various progenies' average values deviate highly significantly from the mean regression line "within progenies".

The variation in the slope of the regression lines in the various progenies is not significant.

The test shows that it is not possible to obtain a good estimate of the average density of the stem with the guidance of the density in the branches by means of a function common to all progenies, even if the average density of the branches in one progeny is calculated for a large number of trees.

A consequence of these population differences is that the correlation coefficient does not increase as much as expected after the change from individual values for the regression to progeny means. The correlations coefficients are summarised here.

	Correlation between basic density in:	
	stem and 1-year-old branch section	stem and 2-year-old branch section
Observed density		
Individual values	0.345	0.487
Progeny mean	0.590	0.526
Relative density		
Individual values	0.335	0.356
Progeny mean	0.571	0.492

When the progeny mean is employed, which seems most realistic in the practical application of branch analyses, the density in the one-year branch sections has the best relationship with the density of the stem. The difference between the observed and the relative basic density is inconsiderable in this respect. Figures 1—4 illustrate this relationship graphically.

4.5 **Applications**

The analysis of co-variation and the graphs for the progeny means in Figures 1—4 show that the accuracy is low when the basic density of the stem is estimated with the aid of the density of the branch sample. It might be possible to give a lower limit for the branch basic density in progenies which are suitable for use in further breeding. Figures 1—4 indicate, however, that such a limit would be set so low that only a few unsuitable progenies would be excluded. This line of enquiry has therefore not been pursued.

In this investigation both the observed and the relative basic density has been analysed. For reasons given in Appdx 2 the relative density gives a clearer expression of the genetically determined density variation and it might therefore have been satisfactory to carry out the analyses using only relative density. The observed basic density was mainly included to make possible a comparison with the values published by Zobel & Rhodes (1956, 1957) which throughout refer to the observed density.

4.6 A comparison between progenies

The question as to whether the differences between the basic density of the various progenies could have arisen by chance or has a real basis was investigated by an analysis of variance. So as to be able to separate the variation which depends on inheritance (progeny) from that which depends on environment (block) a two-way analysis of variance was performed with "Block" and "Progeny" as sources of variation. The calculation of the mean squares and the arrangement of Table 1 and 2 was carried out in accordance with Dixon & Massey (1957, pp. 164—165).

The calculation of variance ratios and the division into components of variance which is shown in Table 3 was carried out on the assumption of "random effects" in the experiment (Peng 1967, p. 80).

A test for interaction between blocks and progeny in no case showed significance.

Otherwise the following variance ratios were obtained:

I. Test of differences between progenies. Hypothesis: no differences. Numerator 24 degrees of freedom and denominator 72 degrees of freedom.

Observed basic density			
Sample	Stem	1-year-old branch section	2-year-old branch section
Variance ratio	3.715***	4.244***	3.645***

Relative basic density			
Sample	Stem	1-year-old branch section	2-year-old branch section
Variance ratio	4.849***	4.151***	4.658***

II. Test of differences between blocks. Hypothesis: no differences Numerator 3 degrees of freedom, denominator 72 degrees of freedom.

Observed basic density			
Sample	Stem	1-year-old branch section	2-year-old branch section
Variance ratio	2.068	1.687	3.160*

Relative basic density			
Sample	Stem	1-year-old branch section	2-year-old branch section
Variance ratio	1.097	1.059	3.850*

Of these (I) shows that the difference between the average basic densities of the progenies was highly significant for all samples.

Between the block means the difference was almost significant (95 per cent level) for the two-year stem section and not significant for the stem and one-year branch section in both measures.

These results show that real differences exist in basic density between progenies both in the stem and in branches even though the density in the branches according to the analysis of co-variance does not vary in the same way as in the stem.

Table 3 shows that the standard deviation of the density within plots and between the progenies' means, respectively, is of the same order for stem samples as for branch samples for both observed and relative basic density.

5 Comparison between progenies and mother trees

5.1 Collection of material

5.1.1 *Background*

When material was to be collected to make possible a comparison between the basic density of mother trees and progenies, mother trees could be found for ten only of the progenies already investigated. Many mother trees had been felled in connection with clear-felling or road construction.

With the cooperation of the Association for Forest Tree Breeding's branch at Brunsberg it was possible to make use of two further progeny trials, namely, No. 20 Apertin and No. 9 Laxå, where in the one case some mother trees had already been subjected to a wood investigation and in the other, all remaining mother trees were easily accessible for sampling.

5.1.2 *Description of progeny trials*

Experiment No. 20 Apertin is situated in Värmland while experiment No. 9 Laxå is in Närke. In what follows, the locations are referred to as Kil and Laxå. Both experiments have in common that they were laid out as plot experiments both comprising progenies from 36 mother trees. The number of replications is four. The spacing is 1.2 m and the planting stock 2 + 0. The forest site type is of the dry dwarf shrub type and the height above sea level is 120 m. Both experimental plots were cleaned in 1961 when the number of stems was reduced to half the original. Further information about the plots:

Locality	Latitude	Plot size (No. Plants)	Planted
Laxå	59°00′	7×7	1946
Kil	59°32′	12×12	1948

Only the 41 progenies have been studied the mother trees of which were available for wood analysis.

According to the plans, the experiments are laid out in the form of incomplete blocks after Yates (1936). The statistical treatment, however, is based on a completely randomised experimental area, i.e. 144 plots are laid out independently of one another. This implies a relatively crude procedure which, however, affects only the possibility of statistically allocating attributing small differences in progenies. The comparison mother tree-progeny is not affected.

5.1.3 *Sampling in the progeny trials*

In the removal of wood samples from the progenies, it was considered to be of great importance to have as representative a selection as possible of the trees which were to remain until the first thinning. At the same time, the sampling procedure involves a considerable risk of damage, which would furthermore affect some progenies only. It was therefore decided that samples should be taken from trees which were to be removed in the cleaning.

In the summer of 1966 the number of stems was reduced all over the experimental area to about a quarter of the original (to 13 trees per parcel at Laxå and 36 at Kil). The cleaning was of the type low thinning and was carried out uniformly over both plots. So that the trees investigated in respect of wood density should have approximately the same diameter distribution as the remaining population, from each parcel in which sampling was to be undertaken the four largest thinnings were chosen. Since there were four replications, wood samples were collected from a total of 16 trees in every progeny.

The following table is a subsequent check to test to what extent this aim was fulfilled:

	Remaining trees	Thinnings	Sampled trees
Laxå			
Arithmetic mean diameter, mm	86.8	65.0	81.2
S.D. of diameter, mm	20.8	20.5	15.3
Kil			
Arithmetic mean diameter, mm	84.3	63.5	89.6
S.D. of diameter, mm	16.5	18.3	16.3

From each of the trees chosen an increment core was removed at a height of about one metre, in a constant direction. The position for boring was moved up or down as required to bring it midway between two branch whorls. The core was removed to the full diameter of the stem by means of an increment borer having an internal diameter of ca 4.5 mm. Thus every annual ring was represented twice. If compression wood was encountered, a new sample was taken at right-angles to the first, which usually avoided the compression wood.

5.1.4 *Sampling from the mother trees*

The mother trees belonging to the trials at Filphus and Kil are widely scattered (in the counties Värmland, Kopparberg and Östergötland), while those for the trial at Laxå are from a single stand, situated about 10 km ENE of Laxå. Information concerning the mother trees is to be found in Persson (1968, Tables 11 & 12).

The mother trees of the Kil trial were bored through the agency of the Association for Forest Tree Breeding in autumn 1965. From each tree at breast height two cores were removed which extended to the pith, on the same line. No comparison trees were bored.

From all the remaining mother trees of the Laxå trial four cores were removed at breast-height at 90° to one another. At least one of these was required to penetrate to the pith. No comparison trees were considered necessary here, since such a large number of mother trees were growing together on the same site.

The ten remaining mother trees of the Filphus trial were bored in the same way as those for Laxå. However, in this case a number of comparison trees was bored along with each mother tree. The number of comparison trees per mother tree was usually six, but was reduced if several mother trees was growing close together. From each comparison tree one core was removed which penetrated to the pith.

5.2 **Laboratory treatment**

The air-dried cores from the progenies were soaked initially for 30 min to soften them. After this, the five latest formed annual rings, represented twice in each core, were removed. From the cores from the mother trees were removed both the five outermost rings and the preceding ten annual rings. The weight and volume of the material was determined according to the method described in Appdx 1. Most of the weighing was done in the laboratory of the Department of Forest Yield. The cores from the mother trees of the Kil trial were, however, analysed at the Brunsberg branch of the Association for Forest Tree Breeding.

For reasons discussed in detail in Section 5.4.3, a further separation was made, as follows:

From the cores of the mother trees of the Kil and Filphus trials were removed a further five sections, each of ten annual rings, beginning from the outside. Thus the last cut lay between the 65th and 66th annual rings from the cambium.

The cores from the considerably older mother trees of the Laxå trial were cut up in such a way that the 90 annual rings immediately inside the 15 rings originally taken were removed; these were not further separated. Then five more sections, each of ten rings, were removed, so that the last cut

lay between the 140th and 141st annual rings from the cambium.

Most mother trees had been bored previously, which had in many cases caused the adjacent wood to become impregnated with resin. Since such a deposit can considerably affect the dry weight, the samples were placed in acetone for four days after separation into sections. The extractive-free samples were then dried and treated in the same way as the sections already analysed.

5.3 **Treatment of data**

All data intended for further treatment were punched on cards. Calculations of the densities and annual ring widths and of the squares and sums of products were carried out on the College's IBM 1401 computer, according to a programme written by the present author. Regression analyses were performed on the same computer with the aid of an existing programme.

5.4 **Relative basic density**

5.4.1 *General*

The reasoning underlying the use of the relative basic density as a measure for causing the genetically determined variation to be expressed in a more basic form than is the case when the observed density is used, is discussed in Appdx 2. In Section 4.3.1 is shown the mode of construction of the regression functions for the relationship between basic density and diameter when age is constant. In the following calculations based on the measurements obtained from the cores, the annual ring width is used as a variable instead of diameter.

5.4.2 *Progeny trials*

The density and average annual ring width for every individual was obtained from the average of the two determinations made (see 5.2).

To test whether the regression of basic density on ring width could be considered as linear, the individuals in each progeny trial were grouped into classes based on mean annual ring width, each class having a width of 0.2 mm. For each class the average basic density was calculated. A graphical check (see Figures 7 & 8) showed that the regression both in the Kil and the Laxå trials, could be considered to be approximately linear. The following equations were obtained in which y represents the relative basic density in g/cm³ for the latest five annual rings, and the mean width for the corresponding annual rings, in tenths of millimetres. The correlation coefficient is denoted by r.

Locality	Equation	r
Laxå	$y = 0.463\,855 - 0.003\,096\,x$	−0.463 (8)
Kil	$y = 0.457\,725 - 0.002\,873\,x$	−0.525 (9)

Then was calculated for every bored tree in the progenies the relative basic density according to the method illustrated above (viz. relative basic density = 100 times the observed basic density/calculated basic density). The mean values obtained for the observed and relative basic density and annual ring widths in the various progenies are compiled in Persson (1968, Tables 13 & 14).

5.4.3 *The mother trees*

As was the case for the progenies, regression functions were constructed for the mother trees for calculating the relative basic density. Since the ten mother trees remaining to the Filphus trial were considered too few to be capable alone of giving a realistic regression function, this material was combined with the 19 mother trees of the Kil trial. This procedure should not involve complications, since the mother trees of both trials originate mainly from the same region. However, it was not considered suitable to include the mother trees of the Laxå trial so as to give a common regression function for all three. The large assemblage of trees on one and the same site at Laxå would probably have influenced the function too greatly.

In the mother tree material from the Kil and Filphus trials, there were marked differences in climate between the sites, mainly in consequence of differences in height above sea level. Numerous investigations have demonstrated that altitude has a marked effect on the basic density, for instance, those of Nylinder & Hägglund (1954), Ericson (1960, 1961, 1966) and Harris (1963). As climatic variables were tried height above sea level, latitude and the mean temperature during the period June—August. This last was calculated with the help of functions constructed by Ångström (1938) and further developed by Ericson (1966, p. 35, 3.2).

A graphical check of the regression of density on annual ring width, illustrated by Figure 5, indicated that it was curvilinear. In the fitting of a suitable function it became evident that the maximum multiple correlation coefficient (R) obtained with the annual ring width to the first power only as a variable, was 0.13. When the square of the annual ring width was introduced, R increased to 0.47.

The fit of the regression was improved only slightly when climate was introduced in some form (R increased from 0.43 to 0.47). Height above sea level alone as climate variable gave as good a fit for the regression as was obtained when latitude was also included. Neither did the calculation of mean temperature, with temperature anomalies according to Ångström (1938) taken into consideration, give a better fit.

Although the climatic effect was not significant, a regression function which included climate was chosen, in view of the fact that its effect on density is well documented in previous investigations.

The function chosen was No. 10 below, which has height above sea level as the climatic variable.

The increment of many mother trees had been very low during the latest five-year period, with many annual ring widths of the order of 0.3—1.0 mm, implying that the formation of starvation wood was to be expected (Ericson 1966, pp. 101—102). That such wood was formed is confirmed by Figure 5, where it is shown that density decreases rapidly with decreasing annual ring width, where this is less than ca 1 mm. There is some risk that starvation wood may begin to form at different annual ring widths in different individuals. It was therefore of interest also to study wood samples having greater ring widths, which was the case for some of the inner sections of the core. For this reason, regression functions were fitted for all the core sections.

In all functions, annual ring width to the first and second power, and height above sea level, were included. The following equations were obtained for the various sections, where No. 1 is the outermost part, comprising five annual rings, and No. 2—7 are the subsequent sections, comprising ten rings each. y is the basic density, g/cm³, x = annual ring width, tenths of millimetres, z = height above sea level, metres.

Section	Equation	R	
1	$y = 0.295873 + 0.142057\,x - 0.041957\,x^2 + 0.000090\,z$	0.469	(10)
2	$y = 0.389281 + 0.073254\,x - 0.027318\,x^2 + 0.000048\,z$	0.316	(11)
3	$y = 0.449279 + 0.042585\,x - 0.018525\,x^2 - 0.000016\,z$	0.265	(12)
4	$y = 0.453880 + 0.023538\,x - 0.010771\,x^2 - 0.000067\,z$	0.222	(13)
5	$y = 0.448027 + 0.037987\,x - 0.017737\,x^2 - 0.000097\,z$	0.382	(14)
6	$y = 0.463935 + 0.022613\,x - 0.012270\,x^2 - 0.000109\,z$	0.360	(15)
7	$y = 0.436720 + 0.047789\,x - 0.029544\,x^2 - 0.000077\,z$	0.524	(16)

For the density of the mother trees of the Laxå trial, similar regression functions were also constructed in which, however, climate, which was the same for all 22 trees, was not included. The average basic densities for various annual ring widths can be seen in Figure 6.

In this material the average annual ring width for the five outermost rings of all trees was between 0.2—1.0 mm, i.e. wholly in the range of widths in which, according

to Ericson, starvation wood is generally formed. The regression of basic density on annual ring width also showed an increase in density with increasing annual ring width. The regression appeared to be generally linear when the separation into classes and calculation of the average were in accordance with previous practice.

In the inner parts of the increment core, larger annual ring widths occurred. This implies that the density in these sections might be thought to decrease with increasing annual ring width. In order to reproduce a curvilinear relationship, the squared ring width was included with the simple in all the regression functions constructed for the seven sections (described in 5.2).

The equations and multiple correlation coefficient (R) obtained were as follows, where y = basic density, g/cm^3 and x = annual ring width, tenths of millimetres.

Section	Equation	R	
1	$y = 0.357973 + 0.156764\,x - 0.052476\,x^2$	0.617	(17)
2	$y = 0.271925 + 0.438805\,x - 0.249694\,x^2$	0.582	(18)
3	$y = 0.457962 + 0.019038\,x + 0.001447\,x^2$	0.159	(19)
4	$y = 0.521558 - 0.125951\,x + 0.083246\,x^2$	0.155	(20)
5	$y = 0.470494 + 0.040728\,x - 0.028712\,x^2$	0.162	(21)
6	$y = 0.399543 + 0.195535\,x - 0.097855\,x^2$	0.418	(22)
7	$y = 0.449897 + 0.060831\,x - 0.040748\,x^2$	0.414	(23)

For all the mother trees included in this investigation the relative basic density was calculated for each one of the seven sections by the method previously indicated (relative basic density = 100 x observed basic density/calculated basic density). The average of the relative density for all sections was calculated similarly for each tree. The data obtained for the mother trees are compiled in Persson (1968, Tables 15—16).

5.5 Progeny differences

A prerequisite for the realistic comparison of the basic density of progenies and mother trees is that there should be real differences in the density of the various progenies in the trial.

As was mentioned in section 4.6, an analysis of variance for the experiment at Filphus showed that there were highly significant differences between the 25 progenies in both observed and relative density.

Since the progenies in the trials at Kil and Laxå could not be regarded as being divided into blocks (see 5.1.2) it was not possible to carry out the analysis of variance according to the two-way model. Instead, the analysis was performed according to Bonnier & Tedin, Chapter 8, Hierarchical division, with the hierarchies "progenies" —"parcels within progenies"—"individuals within parcels".

All three progeny trials were so planned that a division into provenance groups could also be made. The results of processing from the trial at Kil showed, however, no difference in density between the provenance groups (Nilsson 1968). Furthermore, since sampling within provenance groups was incomplete in the present investigation (see 5.1.2), the differences between these groups were not analysed.

The hypotheses tested were that no differences existed "between progenies" and "between parcels". Only the relative density was used. The confidence limits of the tables must be used with some caution, since the transformation to relative density employed a function based on data from all trials.

The analysis of variance is shown in Table 4 and gave for the Kil trial the following result: variance ratio for differences between progenies 5.454***. The hypothesis "no difference" was rejected at the 0.1 per cent level.

The variance ratio for differences between parcels was 1.252. Not significant.

For the Laxå trial was obtained: variance ratio for differences between progenies

2.586**. The hypothesis "no difference" was rejected at the one per cent level. Variance ratio for differences between parcels was 1.124. Not significant.

With the support of these results, the comparisons between mother trees and progenies described in section 5.6 could be made.

In the practical application of selection based on the density of the mother trees, it is of interest not only to establish a statistically defined difference between different progenies, but also to know the order of magnitude of the difference. Hence in the Kil and Laxå trials the components of variance were divided up according to Kempthorne (1957, p. 245), following which the standard deviation of the relative density between the true means of the progenies was calculated. The following values were obtained:

Locality	Standard deviation between true progeny means %
Kil	3.156
Laxå	2.045
Filphus	2.398

As may be seen, there is a larger variation between the progenies in the Kil trial than in the Laxå trial, a difference which might have been expected, in view of the more heterogeneous origin of the progenies at Kil compared with those at Laxå. The standard deviation for the Filphus trial was obtained from Table 3, and is based on analyses of stem disks. All 25 progenies are included. Only the analyses of progenies of the mother trees whose wood was investigated have been used as a base for the values of the other trials.

5.6 **Relationship between basic density in progenies and mother trees**

5.6.1 *Test of significance*

For analysis of the relationship between the relative basic density of the progenies and the mother trees were used both the average relative density of the various progenies and the relative densities of the mother trees.

As was mentioned above, the density in the progenies of the Filphus trial was determined with the aid of stem disks, in contrast to the procedure in the other two trials, where increment cores were used. There is thus a risk that systematic differences may have arisen. Since the relative densities are calculated within each progeny trial—which implies that the relative density of a progeny is determined only as the relation between the individual progeny and the mean for the trial—any such systematic errors will not, however, affect the analyses.

A disturbing factor is that the relationships between the densities of the progenies are not always the same at different sites. This has, for instance, been demonstrated by McKimmy (1966). Such phenomena are not available for analysis in the present material, since no mother tree is represented in more than one progeny trial. The differences in situation between the progeny trial at Kil and that at Filphus, which were united for processing, is 300 m in height and one degree of latitude, thus considerably less than the differences with which McKimmy worked (differences of over 1100 m in height and three degrees of latitude). The amalgamation of the progenies from the Kil and Filphus trials was therefore considered permissible.

The mother trees of these progenies had been amalgamated by means of a calculation of a common regression function for the influence of annual ring width and height above sea level on the basic density (see 5.4.3). The Kil and Filphus material was also studied separately.

The correlation coefficient was used both as a measure of the degree of co-variation and for testing the significance levels of the various relationships. The tests were carried out in accordance with Dixon & Massey (1957, pp. 200—201) by determination of the confidence interval for different levels and by checking that these intervals in their entirety exceeded 0.

Table 5 shows both the correlation coefficients obtained and the significance. In

this context a correlation coefficient was also calculated for the entire material (51 mother trees).

In Table 6 are shown the confidence intervals calculated for the correlation coefficient between the mean of the relative densities for the progeny and for the relative density in the mother tree, calculated as the average of all seven increment core sections.

The averages column in Table 5 shows that the correlation coefficient from the combined Kil and Filphus experiments is highly significantly greater than 0. From Table 6 it may further be seen that the 95 per cent confidence interval is 0.29—0.79. The correlation coefficient was 0.591. The material is graphically presented in Figure 9. The Kil material considered alone gave a correlation coefficient (r) significantly greater than 0, while the Filphus trial did not give r to be significantly greater than 0. Neither was significance obtained in the Laxå trial. The value of r obtained (0.415) lay, however, very close to the lower limit for significance at the 95 per cent level, i.e. $r = 0.43$. This material is presented graphically in Figure 10.

In the calculation of r, 0.31 was the second lowest value obtained, while the lowest, 0.06, was obtained for the comparison between the density of the five outermost rings of the mother trees and the density of the progenies in the Laxå trial. In this case, the average ring width of the mother trees was markedly lowest, viz. 0.6 mm. This implies that there is a large possibility of error, both in the direct measurements and in the calculation of an expression for the regression of density on ring width.

5.6.2 *Selection effects*

It is, of course, of great economic interest to determine what effect selection in respect of the relative density of the wood in the mother trees will give on the density of the wood of the progeny.

An attempt has been made to calculate the probable selection gain by constructing functions for the regression of the progenies' relative density on the density of the mother trees, both for the amalgamated Kil and Filphus material and for the Laxå material. The following functions were obtained when the relative density of the mother trees was given as the average of core sections 1—7. In the equations, y = relative basic density of a progeny and x = the relative basic density of the mother tree. The correlation coefficient is denoted by r and the standard deviation of the relative density between the mother trees expressed in percentage units by σ_x.

Locality	Equation	r	σ_x
Kil – Filphus	$y = 72.2520 + 0.2782\,x$	0.591	7.04 (24)
Laxå	$y = 77.0285 + 0.2296\,x$	0.415	4.72 (25)

On the basis of mother trees having a relative density 100, which approximates to the degree of selection presently applied in the choice of parent trees for seed orchards, the average density for the selected group may be calculated according to the following formula, where m_u = mean value of the group, m = original population's mean value σ = standard deviation of the original population.

$$m_u = m + 2\sigma \cdot \frac{1}{\sqrt{2\pi}} \qquad (26)$$

The original distribution was assumed to be normal. Thus for the Kil-Filphus material, $m_u = 105.62$ was obtained and for the Laxå material $m_u = 103.77$. If these values are substituted in functions 24 and 25 for the Kil and Filphus material, an expected relative density of 101.63 in the progeny is obtained; that for the Laxå material 100.85. The increase in density is thus 1.63 and 0.85 per cent, respectively.

If the degree of selection is refined, so that only the best ten per cent of mother trees in respect of density are chosen, similar calculations (Allard 1960, p. 94) give the result that the expected gain in the average density of the progenies for the Kil and Filphus material is ca 3.5 per cent, and ca 1.9 per cent for the Laxå material. If, furthermore, the father trees are selected

in respect of density, the gain should increase still further.

In assessing these percentages it must, however, be borne in mind that there are many factors of uncertainty in the calculations. For instance, as is shown in 5.6.1 for the Laxå material, the relation between the relative density of the mother trees and the progenies could not be demonstrated to be significantly positive.

The heritability (narrow sense) may, according to Stern (1960 p. 56) and Becker (1957, p. 62), be determined as the regression coefficient in the relationship progeny on parents. If the progenies are obtained after free pollination, as in this case, the doubled regression coefficient for the relationship progeny on mother trees is an estimate of the heritability (Hattemer 1963). In equations 24 and 25, the regression coefficients were 0.278 and 0.230, their standard deviation being 0.073 and 0.113, respectively. An estimate of the heritability thus gives the value 0.56 ± 0.15 for the Kil-Filphus trials and 0.46 ± 0.23 for the Laxå trial.

6 Discussion

It should be emphasised that the relative densities determined for the progenies do not refer to the whole growth period. At the time of investigation, the trees were at most 22 years old and the greater part of the wood which will be harvested during the rotation has thus yet not been formed. The relative density shows some variation between different parts of the stem cross-section. No comparison was made between the density of the innermost annual rings and that in the other wood, partly because the inner parts of the increment cores were often in poor condition.

Partly on the basis of the investigations of Zobel & Rhodes (1956, 1957), referred to in Chapter 3, in which good correlation was obtained between the density in the inner and in the outer annual rings of the same tree, it may be expected that the changes will not be of great importance. One indication that the relationship between the density in the progenies and that in the mother trees should at least not weaken with increasing age of the progenies, is given by Zobel's (1963) finding that the heritability (narrow sense) for species of pine in the southern United States increased with the age of the progenies up to the age of 15 years. Here it should be noted that these pines are very fast-growing, hence parallels cannot be drawn with 15-year-old Swedish pine.

Zobel (1953) also discusses various methods for estimating the heritability. The heritability is often estimated as the relation between the additive genetical variability and the phenotypic variability in a progeny trial, without, however, anything being known about the parent trees. Zobel (1961) points out, amongst other things, that the more uniform is the environment on an experimental area, the greater is the estimated value for the heritability, in that the phenotypic variation decreases.

Heritability determined in this way, valid solely within the specific environment of the experimental area, forms a very uncertain basis for the estimation of the selection gain.

The heritability may also be estimated, as mentioned above, with the aid of the regression of the progenies on the mother trees. As regards the pine species specifically dealt with by Zobel, *Pinus taeda* and *P. elliottii*, such a comparison is complicated by the fact that the young individuals form "juvenile wood", which differs from the wood formed later in that the density is considerably lower and that its variation between individuals less. This implies, according to Zobel (1963), that it is not considered statistically acceptable directly to compare the density of the mother trees and the progenies.

The formation of juvenile wood in the Swedish pine has been very little studied. A calculation based on Figure 5—8 shows that the progenies have on the average an observed basic density from seven to nine per cent lower than that of the mother trees for the same annual ring width. A study of analyses of 78 pines suggested as plus trees showed that the wood formed during the earlier years has a lower basic density (significant at the one per cent level) than the average for the whole tree when differences in annual ring width are taken into consideration. The differences between "juvenile wood" and "mature wood" seem, however, compared with those in the American pine species, to be very small. By calculation of the relative basic density, which involves the use of separate functions for each progeny trial and group of mother trees, possible differences are eliminated.

The standard deviation in relative density between the individuals in the progeny trial at Filphus was 6.3 per cent for the stem samples. This value may be compared with the standard deviation of relative density between the mother trees of the Kil and Filphus trials, which was 7.0 per cent as is discussed in section 5.6.2. The order of magnitude is thus the same. Also in the progeny trials at Kil and Laxå, the standard deviation of the relative basic density for the entire material as calculated on the basis of the analysis of variance in Table 4, lay between six and seven per cent. The standard deviation for the relative basic density between older pines, obtained by Ericson (1960), was of the same order of magnitude, there being three values of 6.3 per cent and one of 5.8 per cent.

In the material studied in the present work, the phenomena which, according to Zobel, make the regression of progeny on parents unsuitable as a basis for an estimate of the heritability, did not occur. This type of regression has therefore been used in estimates of the degree of heritability in section 5.6.2.

The heritability based on the regression of the progenies on the mother trees was doubled with regard to the fact that the progenies arose after open pollination. This calculation is based on the assumption that the relative density of the father trees both varies independently of that for the mother trees and that it is, on the average, similar to the relative density of the mother trees, viz. 100 per cent. The latter assumption should be acceptable, since the density was not used as a criterion in the choice of mother trees. There is, however, a danger that trees within certain areas have generally a high or a low relative density. This may depend on provenance effects or on a local climate which is not fully explained by the climatic variable employed, namely, height above sea level. Such a difference between localities implies, for instance, that mother trees in a locality having a high density have a considerable chance of being pollinated by trees which, on the average, also have a high density. In this way there is a risk that the heritability may be overestimated. Thus the heritability (0.56) determined for the Kil-Filphus trial may be suspected to have been systematically overestimated.

It follows from this reasoning that it would be possible to determine the heritability with greater certainty if the father trees were known. Recently, the layout of progeny trials in Sweden has been increasingly concentrated to controlled crosses. Most of these trials are, however, still far too young for valid investigation of the wood. Future studies of these and similar progeny trials should be capable of giving considerably more information about the inheritance of density than would be given by extended studies of progenies arising from free pollination. Through the study of controlled crosses it should be possible to assess the effects which can be attained within seed orchards of selected plus trees. Since 1960, all proposed plus trees have been tested in respect of density. Only trees having a relative density of at least ca 100 per cent are chosen for use in seed orchards.

In tree breeding, naturally not only the relative basic density is to be considered. Many other properties seem to have greater economic importance, for instance, growth rate and branch quality. Selection on the basis of these factors lies outside the purview of the present work, but cannot for this reason be ignored. If a positive selection based on the relative density were to involve a negative effect on the growth rate, that selection would be in vain. Investigations reported by Zobel (1963) indicate that the risks for this are small as regards some American species of pine.

Ericson (1960, Table 1), has compared in a Swedish material of pine the basal area of an investigated tree with the total basal area within a radius of five metres of the tree. No relationship could be demonstrated between the relative density of a tree and the proportion which it occupied of the total basal area. From this it may be concluded that a high relative density is not obtained at the expense of the increment of the surrounding trees, and probably not at

the cost of production per unit area.

In the progeny trials at Kil and Laxå, the basal area has been calculated for the trees remaining after clearing. For each progeny the relative total basal area has then been calculated as the observed total basal area for the progeny expressed as a percentage of the average basal area for the progenies. If the correlation coefficient (r) for the relation between the relative total basal area for the progenies and the relative basic density for the mother trees is calculated, for the Laxå trial is obtained $r = -0.28$ and for the Kil trial, $r = -0.07$. Neither of these correlation coefficients differs significantly from 0. The 95 per cent confidence interval about $r = -0.28$ has the limits $+0.16$ and -0.62, respectively, for the 22 pairs of values of the Laxå trial. Hence there is nothing to contradict the assumption that density and growth rate vary independently. Neither can it be demonstrated that a mother tree with a high relative density has given progenies with low growth capacity. This does not, however, mean that the relationship between density and growth rate should be not studied further.

This investigation shows that a selection of the mother trees in respect of density can give a clear effect in the average density of the progenies. At the same time, the difficulties of separating, on the basis of phenotype, trees having an especially good genotype as regards branch quality and growth rate, should be borne in mind. It is, therefore, possible that a very strong selection, based on density and carried out amongst a large number of trees chosen on the basis of acceptable branch quality and increment, might be the right way to attain rapid and good results.

Summary

The present work is based on a thesis submitted for the degree of Licentiate at the Department of Forest Yield, Royal College of Forestry, entitled "Studie över torr-råvolymvikten hos moderträd och avkommor av tall", which was published in 1968.

The work is intended to elucidate whether there is a relationship between the basic density in mother trees of pine and progenies arising from open pollination.

To facilitate determination of the density in progenies at as low an age as possible, it was first investigated whether the basic density in the stems of young pine trees could be calculated by means of a regression function after the determination of the basic density in branches.

On the basis of a close study of 20 young pines, wood samples were taken from branches in the uppermost whorl, from two-year-old branch sections in the second branch whorl from above and from a six-year-old stem section, all from 500 pines belonging to 25 progenies in a comparative progeny trial.

The relative basic density was calculated for every sample as the observed basic density/calculated basic density, expressed in per cent. The calculated density was obtained by means of a function for the relationship between basic density and diameter.

A co-variance analysis of the basic density in the stem and the density in one-year-old and two-year-old branches gave the result that the mean values for the progenies differed significantly from the mean regression.

The slopes of the regression lines of the various progenies did not differ significantly from one another.

The analysis gave the same result both when the observed and when the relative density was employed.

By means of the first result it was shown that the various progenies belong to different populations in respect of the relationships tested.

On the basis of the analysis of co-variance, the method employing branch analyses was concluded to have little value.

The analysis of variance showed that there were significant differences "between progenies" in all three parts of the tree for both observed and relative basic density.

In order to be able to carry out a comparison between the basic density of mother trees and progenies, the density was determined in ten of the mother trees of which the wood of the progenies had been investigated. Furthermore, samples were taken from two other comparative progeny trials arising after free pollination, in the one case from 22 and in the other from 19 progenies, as also from the mother trees of the progenies. The relative basic density was calculated for both mother trees and progenies.

The analysis of variance showed significant differences in the relative basic density between various progenies in the trials investigated.

The comparison between the relative basic density of the mother trees and their progenies gave in one case a correlation coefficient of 0.591*** (29 pairs), in another case 0.415 (22 pairs, not significant). The density was in no case a criterion in the choice of mother trees. A calculation was made of the increase in the average density of the progenies attained by application of a degree of positive selection of 50 per cent and indicated that in the one case the relative density would have increased by 1.6 per cent and in the other by 0.9 per

cent . For a positive degree of selection of ten per cent the percentage 3.5 and 1.9 would have been obtained.

Calculation of the heritability (H) on the basis of the regression of progenies on mother trees gave in the one case $H = 0.56 \pm 0.15$ and in the other case $H = 0.46 \pm 0.23$.

Acknowledgements

My grateful thanks are due to the head and staff of the Department of Forest Yield, Royal College of Forestry, where most of the work reported here was done .

I also gratefully acknowledge the help of the following persons: Professor Per Nylinder, Dr Olle Persson, Professor Enar Andersson and Dr Bo Nilsson, all of the Royal College of Forestry.

Literature

Allard, R. W. 1960. Principles of plant breeding. — John Wiley & Sons. New York, London.

Ångström, A. 1938. Temperatur och temperaturanomalier i Sverige 1901—1930. (Temperature and temperature anomalies in Sweden 1901—1930.) — Medd. Meteorologisk-Hydrografiska Anst., Stockh. 7(2).

Becker, W. A. 1967. Manual of procedures in quantitative genetics. — Seconded. Washington.

Bonnier, G. & Tedin, O. 1940. Biologisk variationsanalys. — Upplaga I. Stockholm.

van Buijtenen, J. P. 1962. Heritability estimates of wood density in Loblolly pines. — Tappi 45(7), 602—605.

Dixon, W. J. & Massey, F. J. 1957. Introduction to statistical analysis. — Second edition. McGraw-Hill Book Company. New York, Toronto, London.

Eklund, B. 1951. Undersökningar över krympnings- och svällningsförändringar hos borrspån av tall och gran. Investigations of the shrinkage and swelling changes in increment cores of pine and spruce.) — Medd. SkogsforsknInst. Stockh. 39(7), 1—59.

Ericson, B. 1959. A mercury immersion method for determining the wood density of increment core sections. — Rapp. Avd. Skogsprod. SkogsforsknInst., Stockh. No. 1.

— 1960, Studies of the genetical wood density variation in Scots pine and Norway spruce (Studier över den ärftliga volymviktsvariationen hos tall och gran.) — Rapp. Avd. Skogsprod. SkogsforsknInst., Stockh. No. 4.

— 1961. Skogsträdsförädling med sikte på ökat massautbyte. Några preliminära forskningsresultat. — Medd. SkogsforsknInst., Stockh. (Ser. Uppsatser) Nr 81. (Särtryck ur Teknisk-Vetenskaplig Forskning 32 (1961):4, 194—203.)

— 1966. Determination of basic density in small wood samples. An examination of some sources of error. — Rapp. Uppsats. Instn. Skogsprod. Skogshögsk., Stockh. Nr 9.

— 1966. Gallringens inverkan på vedens torrråvolymvikt, höstvedhalt och kärnvedhalt hos tall och gran. (Effect of thinning on the basic density and content of latewood and heartwood in Scots pine and Norway spruce.) — Rapp. Uppsats. Instn. Skogsprod. Skogshögsk., Stockh. No. 10.

Goddard, R. E. & Cole, D. E. 1966. Variation in wood production of six-year-old progenies of select Slash pines. — Tappi 49(8), 359—362.

Goggans, J. F. 1964. Correlation and heritability of certain wood properties in Loblolly pine (Pinus taeda L.). — Tappi 47(6). 318—322.

Harris, J. M. 1963. The influence of environment on the wood density of Radiata Pine grown in New Zealand. — FAO World Consult. For. Genet., Stockholm 1963. No. FAO/FORGEN 63/ — 7/3.

— 1965. The heritability of wood density. — In Proc. Mtg. Sect. 41 Int, Union For. Res. Organ. Melbourne 1965, Vol. 2.

Hattemer, H. H. 1963. Estimates of heritability published in forest tree breeding research. — FAO World Consult. For. Genet., Stockholm 1963. Vol. 1. 2a/3.

Jackson, L. W. R. & Warren, B. J. 1962. Variation and inheritance in specific gravity of Slash and Loblolly pine progeny. — Res. Pap. Ga. For. Res. Counc. No. 14.

Kempthorne, O. 1957. An introduction to genetic statistics. — John Wiley & Sons, New York.

Matern, B. 1955. Kompendium i statistik, Del I. — Skoghögskolans kompendiekommitté, Stockholm.

McKimmy, M. D. 1966. A variation and heritability study of wood specific gravity in 46-year-old Douglas Fir from known seed sources. — Tappi 49(12), 542—549.

Nilsson, B. 1968. Studier av några kvalitetsegenskapers genetiska variation hos tall (Pinus silvestris L.). (Studies of the genetical variation of some quality characters in Scots Pine (Pinus silvestris L.). — Rapp. Uppsats. Inst. för skogsgenetik. Skoghögskolan, Stockholm No 3.

Nylinder, P. & Hägglund, E. 1954. Ståndorts- och trädegenskapers inverkan på utbyte och kvalitet vid framställning av sulfitmassa av gran. (The influence of stand and tree properties on yield and quality of sulphite pulp of Swedish spruce (Picea excelsa).) — Medd. SkogsforsknInst., Stockh. 44(11).

Peng, K. C. 1967. The design and analysis of scientific experiments. — Addison-Wesley, Reading, Mass.

Persson, A. 1968. Studier över torr-råvolymvikten hos moderträd och avkommor av tall. — Lic. avh. Inst för skogsproduktion, Skoghögskolan, Stockholm.

Squillace, A. E., Echols, R. M., Dorman. K. W. 1962. Heritability of specific gravity and summerwood per cent and relation to other factors in Slash pine. — Tappi 45(7), 599—601.

Stern, K. 1960. Plusbäume und Samenplantagen. — J. D. Sauerländer's Verlag, Frankfurt am Main.

Stonecypher, R. W. 1966. Estimates of genetic and environmental variances and covariances in a natural population of Loblolly pine (Pinus taeda L.). — Technical Bulletin, Southlands Experiment Forest, Bainbridge, Ga. No. 5, 1966, p. 128.

Stonecypher, R. W. & Zobel, B. J. 1966. Inheritance of specific gravity in five-year-old seedlings of Loblolly pine. — Tappi 49(7), 303—305.

Yates, F. 1936. Variety trials involving a large number of varieties. — Journ. Agric. Science XXVI.

Zobel, B. 1960. Selection and breeding of coniferous trees with superior wood characteristics. — 5th World Forest Congr. Seattle, Washington.

— 1961. Inheritance of wood properties in conifers. — Silvae Genet. 10, p. 65.

— 1963. Breeding for wood properties in forest trees. — FAO World Consult. For. Genet., Stockholm 1963. 7/0.

Zobel, B. & Rhodes, R. 1956. Specific gravity estimations of mature Loblolly pine from juvenile wood and seedling limb sections. — Forest Science, Vol. 2, June 1956, Number 2.

— 1957. Specific gravity indices for use in breeding Loblolly pine. — Forest Science, Vol. 3. Sept. 1957, Number 3.

Sammanfattning

Arbetet avsåg att undersöka, om något samband finns mellan torr-råvolymvikten hos moderträd av tall och hos avkommor efter fri avblomning.

För att möjliggöra en bestämning av volymvikten hos avkommorna vid så låg ålder som möjligt, undersöktes först om torr-råvolymvikten i de unga tallarnas stammar kunde beräknas genom en regressionsfunktion efter bestämning av torr-råvolymvikten i grenar.

På grundval av en ingående undersökning av 20 unga tallar togs vedprov från gren i översta grenvarvet, 2-årig grendel i 2:a grenvarvet uppifrån samt 6-årig stamdel, allt från 500 tallar, tillhörande 25 avkommor i ett jämförande avkommeförsök.

Relativ torr-råvolymvikt beräknades för varje prov som observerad torr-råvolymvikt/beräknad torr-råvolymvikt uttryckt i procent. Den beräknade volymvikten erhölls genom en funktion över sambandet mellan torr-råvolymvikt och diameter.

Kovariansanalys av torr-råvolymvikt i stam och volymvikt hos 1-åriga respektive 2-åriga grenar, gav till resultat:

Avkommornas medelvärden avvek signifikant från den genomsnittliga regressionen.

Lutningarna hos de olika avkommornas regressionslinjer avvek ej signifikant från varandra .

Analysen gav samma resultat både vid användande av observerad och av relativ volymvikt.

Genom det första av resultaten visades, att de olika avkommorna hör till olika populationer med avseende på de testade sambanden .

På grundval av kovariansanalysen bedömdes metoden med grenanalyser ha ringa värde.

Genom variansanalys konstaterades därefter att signifikanta skillnader förelåg "mellan avkommor" hos samtliga tre träddelar för både observerad och relativ torr-råvolymvikt.

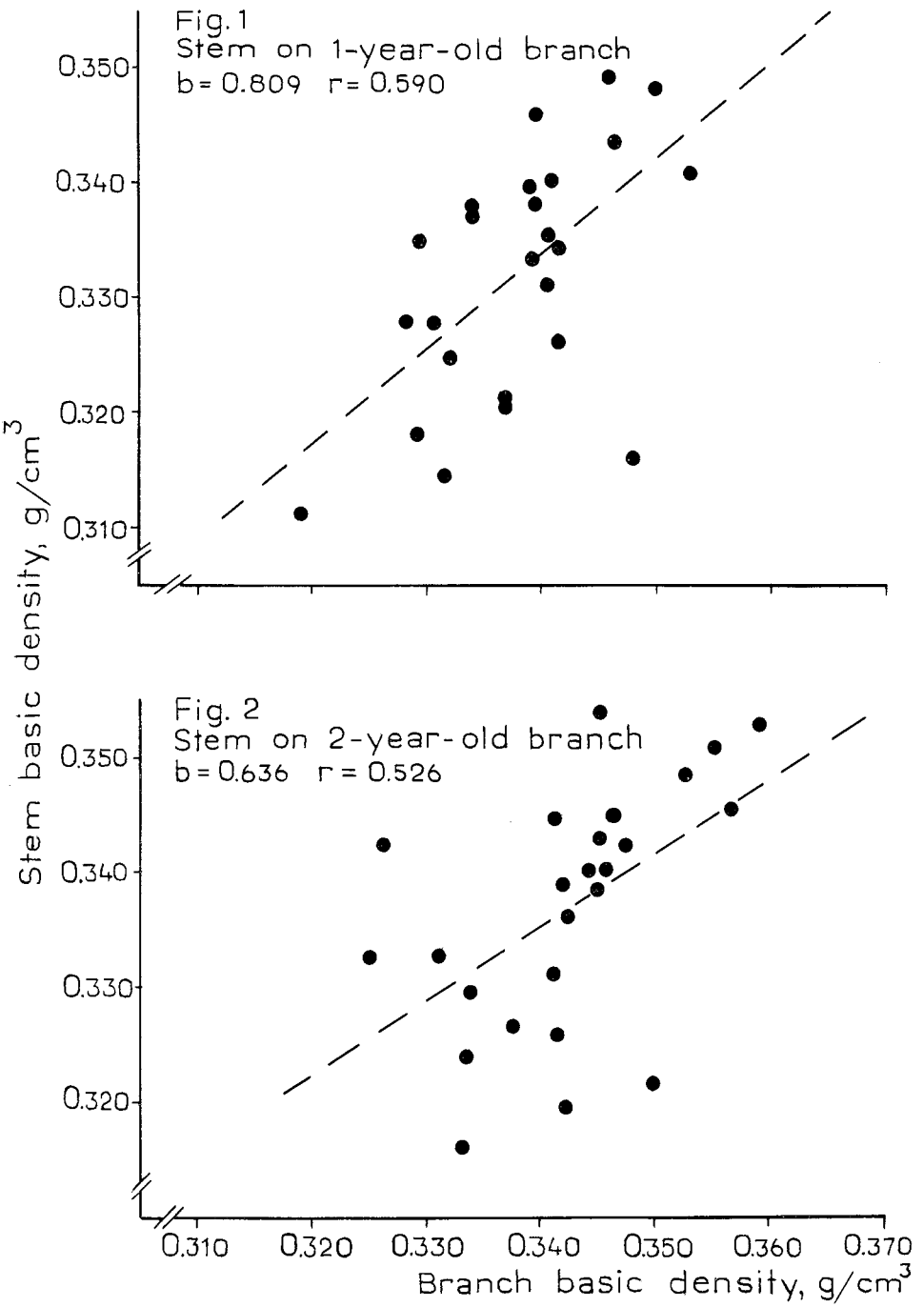
För att kunna genomföra en jämförelse mellan torr-råvolymvikten hos moderträd och hos avkommor, bestämdes volymvikten hos 10 av moderträden till de tidigare vedundersökta avkommorna . Dessutom togs från två andra jämförande avkommeförsök efter fri avblomning vedprov från i ena fallet 22, i det andra 19 avkommor, liksom från avkommornas moderträd. Beräkning av relativ torr-råvolymvikt utfördes för både moderträd och avkommor.

Variansanalys visade signifikanta skillnader i relativ torr-råvolymvikt mellan olika avkommor inom härvid nytillkomna försök.

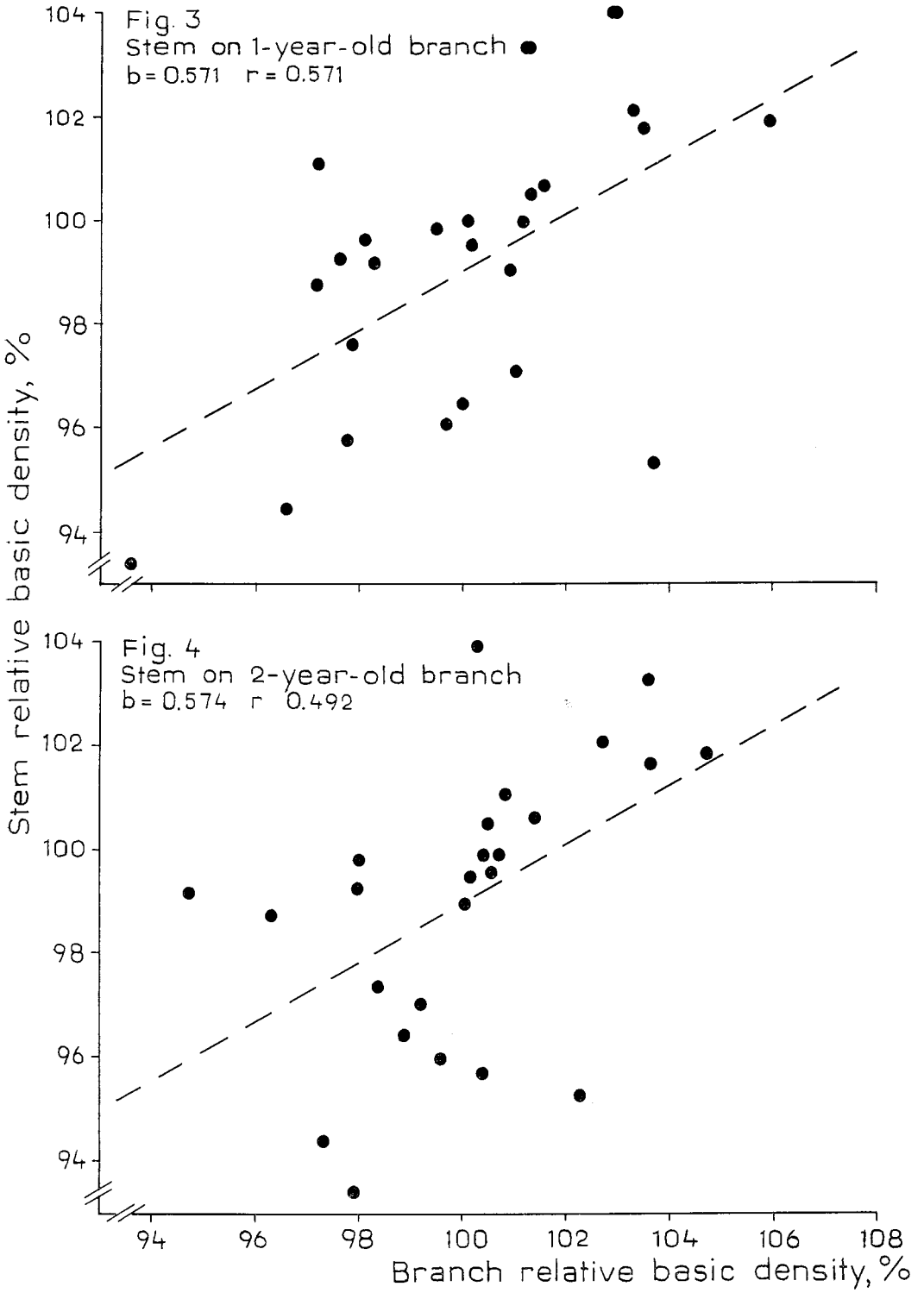
Jämförelsen mellan relativa torr-råvolymvikten hos moderträd och hos deras avkommor gav i ett fall en korrelationskoefficient av 0,591*** (29 värdepar), i ett annat 0,415 (22 värdepar, ej signifikant). Volymvikten har ej i något fall legat till grund för urvalet av moderträd. En beräkning av vilken höjning av avkommornas genomsnittliga volymvikt som erhållits om en positiv selektionsgrad av 50 % hade tillämpats, gav till resultat att i ena fallet hade relativa torr-råvolymvikten ökat med 1,6 %, i det andra med 0,9 %. Vid en positiv selektionsgrad av 10 % hade procenttalen 3,5 respektive 1,9 erhållits.

Beräkning av heritabiliteten (H) på grundval av regressionen av avkommor på moderträd gav i ett fall $H = 0{,}56 \pm 0{,}15$, i ett annat $H = 0{,}46 \pm 0{,}23$.

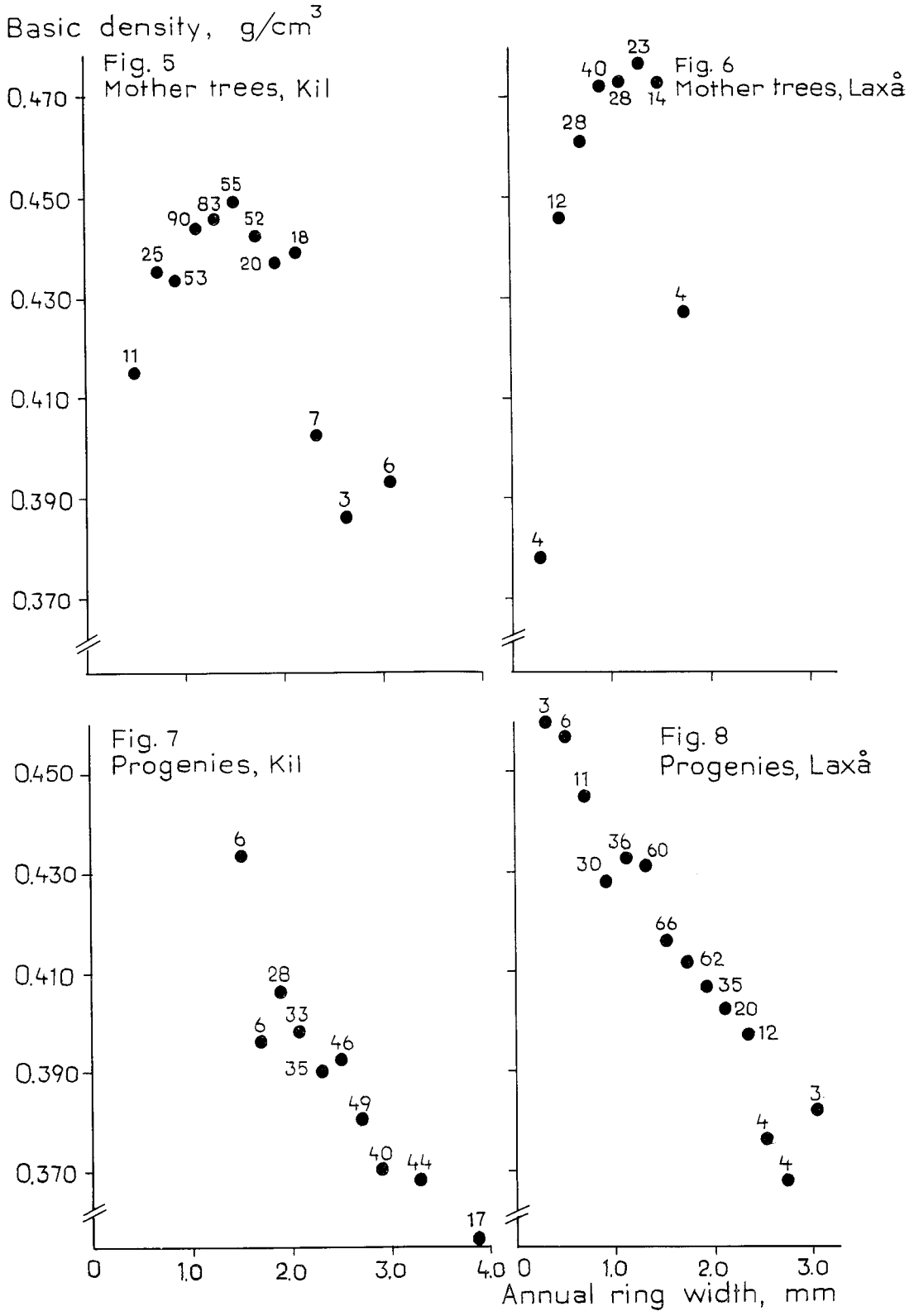
Figures



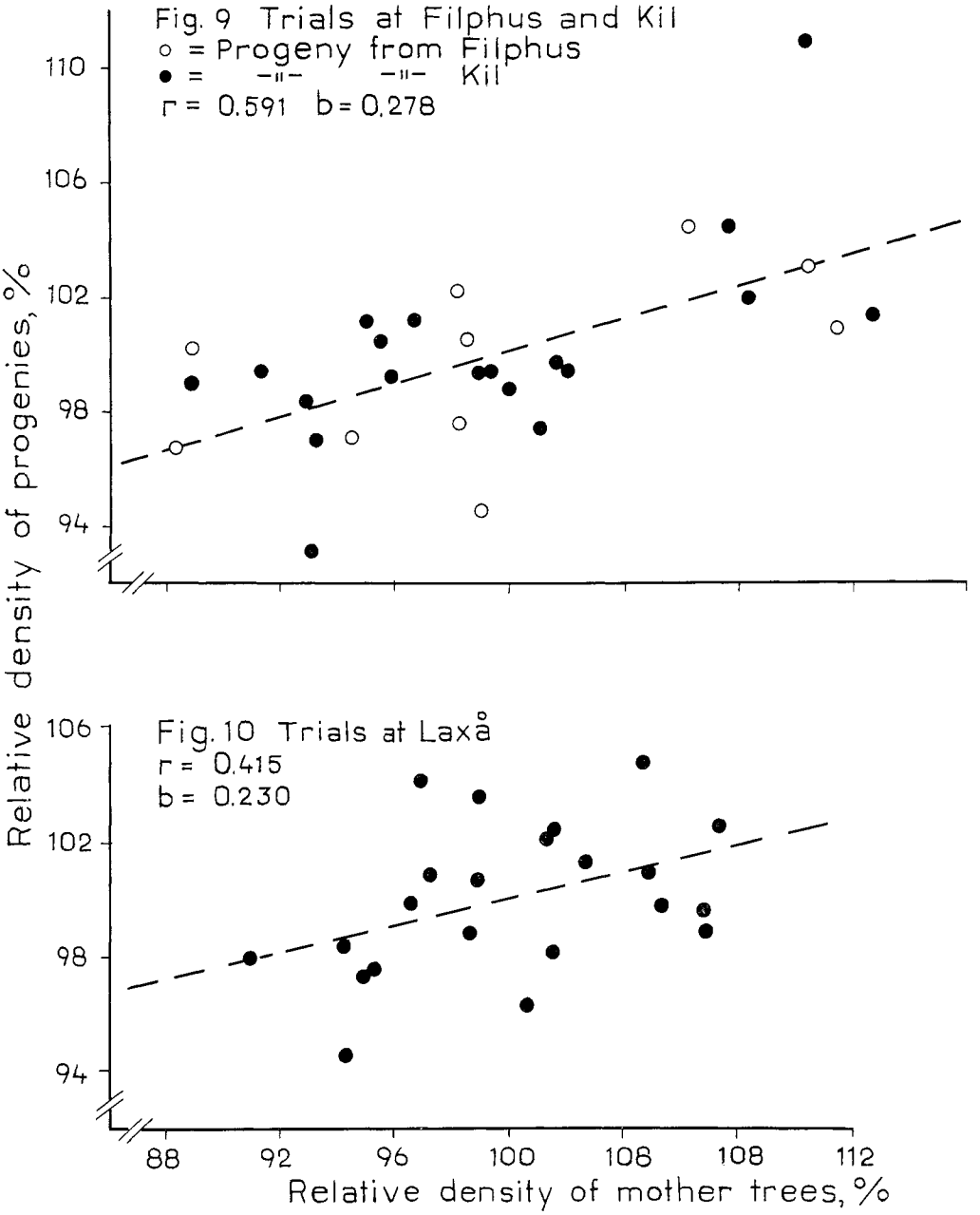
Figures 1–2. Comparison between observed basic density in the stem (dependent variable) and branches (independent variable) in Expt. No 48, Filphus. Each point represents a progeny mean. Correlation coefficient = r, regression coefficient = b.



Figures 3–4. Comparison between basic density in the stem (dependent variable) and branches (independent variable) in Expt. No 48, Filphus. Each point represents a progeny mean. Correlation coefficient = r, regression coefficient = b.



Figures 5–8. Variation of basic density with annual ring width. Illustrated with the aid of ring width classes followed by calculation of average class densities. The figures accompanying each point give the number of individual values on which the average is based.



Figures 9–10. Comparison between the average progeny basic densities after open pollination (dependent variable) and the relative density of their mother trees (independent variable). Correlation coefficient = r, regression coefficient = b.

Tables

Table 1. Analysis of variance in Expt. No 48, Filphus. Observed basic density, g/cm³.

Source of variation	D.F.	Stem		1-year-old branch		2-year-old branch	
		Sum of squares	Mean square	Sum of squares	Mean square	Sum of squares	Mean square
Between progenies	24	0.0548730	0.00228638	0.0291816	0.00121590	0.0374711	0.00156130
Between blocks	3	0.0038175	0.00127250	0.0014501	0.00048337	0.0040604	0.00135347
Interaction	72	0.0443092	0.00061541	0.0206282	0.00028650	0.0308400	0.00042833
Sum	99	0.1029997		0.0512599		0.0723715	
Within parcels	400	0.2037228	0.00050931	0.1050436	0.00026261	0.1514298	0.00037858
Total sum	499	0.3067225		0.1563035		0.2238013	
$F_{interaction}$		$\frac{61541}{50931} = 1.208$		$\frac{28650}{26261} = 1.091$		$\frac{42833}{37858} = 1.131$	
$F_{progenies}$		$\frac{228638}{61541} = 3.715***$		$\frac{121590}{28650} = 4.244***$		$\frac{156130}{42833} = 3.645***$	
F_{blocks}		$\frac{127250}{61541} = 2.068$		$\frac{48337}{28650} = 1.687$		$\frac{135347}{42833} = 3.160*$	

Table 2. Analysis of variance in Expt. No 48, Filphus. Relative basic density, per cent.

Source of variation	D.F.	Stem		1-year-old branch		2-year-old branch	
		Sum of squares	Mean square	Sum of squares	Mean square	Sum of squares	Mean square
Between progenies	24	3582.65	149.277	3583.10	149.296	2738.95	114.123
Between blocks	3	101.32	33.773	114.28	38.093	282.94	94.313
Interaction	72	2216.58	30.786	2589.57	35.966	1763.91	24.499
Sum	99	5900.55		6286.95		4785.80	
Within parcels	400	13970.80	34.927	13430.00	33.575	11733.20	29.333
Total sum	499	19871.35		19716.95		16519.00	
Interaction and within parcels	472	16187.38	34.295			13497.11	28.596
$F_{interaction}$		$\frac{30.786}{34.927} = 0.881$		$\frac{35.966}{33.575} = 1.071$		$\frac{24.499}{29.333} = 0.835$	
$F_{progenies}$		$\frac{149.277}{30.786} = 4.849***$		$\frac{149.296}{35.966} = 4.151***$		$\frac{114.123}{24.499} = 4.658***$	
F_{blocks}		$\frac{33.773}{30.786} = 1.097$		$\frac{38.093}{35.966} = 1.059$		$\frac{94.313}{24.499} = 3.850*$	

Table 3. Estimation of standard deviations in subgroups (=parcels) and between progeny means in Expt. No 48, Filphus.

Standard deviation	Observed basic density, g/cm³			Relative basic density, %		
	Stem	1-year-old branch	2-year-old branch	Stem	1-year-old branch	2-year-old branch
Within parcels	0.0226	0.0162	0.0195	5.910	5.795	5.416
Between progeny means	0.00914	0.00682	0.00753	2.398	2.381	2.068

Table 4. Analysis of variance in the progeny trials at Kil and Laxå. Relative basic density, per cent.

Site	Source of variation	D.F.	Sum of squares	Mean square
Kil	Between progenies	18	3512	195.111
	Within „	285	8556	30.021
	Between parcels	57	2039	35.772
	Within „	228	6517	28.583
	Sum	303	12068	39.828
Laxå	Between progenies	21	2292	109.143
	Within „	330	12702	38.491
	Between parcels	66	2786	42.212
	Within „	264	9916	37.561
	Sum	351	14994	42.718
Kil	$F_{progenies} = \frac{195.111}{35.772} = 5.454^{***}$			
	$F_{parcels} = \frac{35.772}{28.583} = 1.252$			
Laxå	$F_{progenies} = \frac{109.143}{42.212} = 2.586^{**}$			
	$F_{parcels} = \frac{42.212}{37.561} = 1.124$			

Table 5. Correlation coefficients for the regression of relative basic density (average for each progeny) on the relative density in the relative density in the mother trees. The significance level for $r = 0$ is given for each value. The numbering of sections is explained in Section 5.4.3.

Progeny trial	No.	Part No. in mother tree							Average
		1	2	3	4	5	6	7	1–7
Kil + Filphus	29	0.448*	0.520**	0.469***	0.556**	0.563**	0.518**	0.527**	0.591***
Kil	19	0.423	0.500*	0.481*	0.607**	0.590**	0.624**	0.566**	0.627***
Filphus	10	0.612	0.570	0.459	0.448	0.537	0.417	0.487	0.544
Laxå[1]	22	0.055	0.362	0.313	0.367	0.458*	0.455*	0.417	0.415
Kil + Filphus + Laxå	51								0.604***

[1] Lower limit for 95 per cent level: r = 0.43

Table 6. Confidence interval at 5 per cent and 1 per cent level for the correlation coefficients in Table 5, column "Average 1—7".

Progeny trial	95 % confidence interval		99 % confidence interval	
	min	max	min	max
Kil + Filphus	0.29	0.79	0.17	0.83
Kil	0.25	0.84	0.10	0.88
Filphus	—0.14	0.87	—0.35	0.92
Laxå	—0.00	0.71	—0.14	0.78
Kil + Filphus + Laxå	0.31	0.71	0.23	0.75

Appendices

Appendix 1

Determination of the basic density of wood samples

The wood samples analysed in the present work may be placed in three groups in respect of laboratory treatment:

1. Stem sections in the form of ca 5 mm thick disks . Were removed from trees studied in respect of density in stem and branches.
2. Branch samples in the form of ca 5 cm long branch sections.
3. Increment cores ca 4.5 mm in diameter.

Samples in group 1 were not permitted to dry out before the determination of volume, which was carried out by the water displacement method. They were then dried in a thermostatically controlled oven at 103° C for three days, after which they were immediately weighed.

The water displacement method of determining the volume of wood samples is less suited to small samples, because of the tendency of water to adhere to them and because of its low density. The volume of samples in groups 2 and 3 was therefore determined by mercury displacement according to a method described by Ericson (1959) and used routinely for determination of the volume of increment cores at the Department of Forest Yield, Royal College of Forestry. The sources of error in the method have also been studied by Ericson (1966).

Because of the danger of mercury poisoning, samples have to be dried in the oven before being immersed in mercury. After drying and immediate weighing, the samples were allowed to swell in water. For group 3 (increment cores), one hour's immersion was considered sufficient. According to Eklund (1951), increment cores have attained practically their full green volume after this length of time. However, Eklund's results could not be directly referred to group 2 (branch samples), which have their fibres orientated parallel to the long axis of the sample. In the absence of a specific study of the method, it was assumed that these samples, too, would after soaking to fibre saturation point at least have attained their full green volume.

To discover how long soaking was required for the branch samples, a preliminary investigation was performed. The volume of a number of samples was determined after different lengths of soaking. On the basis of the results obtained, it was decided that one-year-old samples should be soaked for two days, while older samples required at least four days' soaking.

Appendix 2

Relative basic density

In assessing the usefulness of basic density as a measure of quality in forest tree breeding, it is important to know which factors influence its magnitude. A compilation by Ericson (1961) indicates that annual ring width is the factor which most strongly influences the basic density of spruce . Increasing annual ring width implies lower density. Latitude, diameter and site class are positively, summer mean temperature and humidity negatively, correlated with density.

If the regression function for a material is estimated, then for a tree under known environmental conditions and with a known annual ring width it is possible to estimate the expected value of the basic density. The estimated value is named the *calculated* basic density, Y_{ber} according to Ericson

(1960). The value observed in the tree is named Y_{obs}.

The value of the expression $100 \times Y_{obs}/Y_{ber}$ is called the *relative basic density,* and is a measure of the deviation of the observed basic density from the regression line.

Ericson found that when he used a regression function based both on the mean temperature for the period June—August and the average annual ring width, the relative basic density did not co-vary to any notable extent with any studied site, stand or tree characteristics (latitude, height above sea-level, site quality class, tree age, tree height, etc.). By contrast, in a comparison with other clones there was a positive, significant correlation between the relative basic density of the tree of origin and that of the clones. This indicates that the relative basic density is a useful measure of the *genetically* determined density.

The intention was to calculate the relative density for all groups of material in the present study. As regards the preliminary investigation, (4.1) it appeared that the relationship between the basic density and the annual ring width was too weak for it to be possible to construct a function. The correlation coefficient for the relationship did not exceed 0.2 for any part of the tree investigated. The calculation of the relative density for the material of the preliminary investigation was therefore omitted.

For all other groups of material, the relative density was calculated for each sample in accordance with the method described in the text.